THE SIGNIFICANCE OF VEGETATIVE REPRODUCTION IN QUERCUS

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The regenerative powers of various species of oaks have been noted by a great many writers, but the role of rhizomatous activity has received little more than descriptive treatment incidental to taxonomic work or ecological characterization of vegetation containing scrub oaks. Jepson (1910) described stump sprouting of California oak trees at some length. Camus (1936) merely noted its common occurrence in the genus.

Numerous authors have described briefly the rhizomatous habits of individual species. Small (1897) wrote, "The habit of *Quercus minima,* with its underground stems, and low erect branches which are usually much less than one meter in height, is enough to separate it specifically from the gigantic forest tree *Quercus virginiana.*" Sudworth (1908) said of the California *Quercus Breweri,* " . . . its network of creeping roots [rhizomes], from which sucker-like stems originate, making irresistible barriers to run-off waters." Viciosa (1950), treating the Spanish species, ascribed to *Quercus pyrenaica,* "Roots deep, accompanied by others superficial and copiously stoloniferous about the trunk." He describes *Quercus Ilex* as follows: " . . . or a shrub, with the root system strongly and deeply developed, carrying moreover lateral and shallow roots much extended, producers of abundant *retoños.*"[2]

Muller (1946) pointed out the survival value of *retoños* in *Parthenium argentatum* (guayule) and that of tillers in *Parthenium incanum* (mariola), both of which are shrubs of semi-arid habitats in western Texas and adjacent Mexico. The tillering of mariola approaches the rhizomatous habit and sometimes produces thickets several meters in diameter, holding almost in perpetuity the site occupied by a short-lived original plant.

The rhizomatous nature of some species of *Quercus* has similar ecological significance, and it is furthermore on occasion a matter of great taxonomic import. It is the purpose of this paper to describe the habits of several illustrative species, to evaluate the ecological significance of the habits, and to record observations upon the taxonomic meaning of habital differences and their evolutionary importance.

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[2] The Spanish word *retoño* denotes a shoot arising from an adventitious bud on an exposed root or underground stem, usually at greater or less distance from the trunk of the parent plant.

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Bush Habit of Quercus Hinckleyi

Quercus Hinckleyi Muller is a low shrub scarcely 0.5 meter in height. It was recently described (Muller, 1951) on the basis of the only known occurrence, a single patch of fewer than 100 plants covering less than 500 square meters at the western edge of the Solitario Basin in southeastern Presidio County in western Texas. The species is associated with sparse grasses and desert shrubs on dry slopes of thin gravelly loam in a transitional zone between grassland and desert. The habitat is distinctly arid and characterized by wide spacing of plants and infrequent establishment of seedlings of any woody species. No seedlings or even young plants of *Q. Hinckleyi* were found. The general region of its occurrence has been searched over a period of years by collectors of oaks so that the restriction of the species to one or a few very limited areas may be accepted as fact. Its relict nature is indicated; the existing population is likely the survival of a more extended range during less xeric periods of the recent geologic past.

The persistence of such a narrowly limited relict species immediately poses questions concerning its means of survival. The species is highly xeromorphic, its tiny leaves being thick, spiny, persistent, and heavily cutinized. Its slow growth and low stature conform with the habits of other species of arid climates where damage is inflicted upon any species whose stature overreaches its water supply.

The aerial stems of *Quercus Hinckleyi* are not long-lived. Ring counts established the largest ones at seven to nine years old. Excavations of a few shrubs revealed a distinctly rhizomatous habit involving short rhizomes. These issued as branches below the soil surface from the bases of erect stems or from older rhizomes (fig. 1) and grew laterally for distances of 4 to 15 cm. They bore reduced (scale) leaves at their nodes and lacked chlorophyll throughout. Upon reaching the soil surface, the rhizomes produced normally expanded and green leaves, and independent rooting followed within a year or two. Each individual clump was observed to consist of several to many ascending stems all springing from one or more old, thick rhizomes in a relatively small soil area, usually a circle 1 to 3 dm. in diameter. The slow spread of the rhizomes has increased the number of individuals by fracture due to death of connecting shoots.

This habit quite clearly explains the ability of the species to persist without the establishment of seedlings. Although some seedling establishment may have occurred in recent centuries, it is not necessary to assume any since the last pluvial period of the Pleistocene. In fact, the entire population is so strikingly uniform in the expression of its genetic characters that it appears almost certain that there is represented only a single clone the age of which is very great.

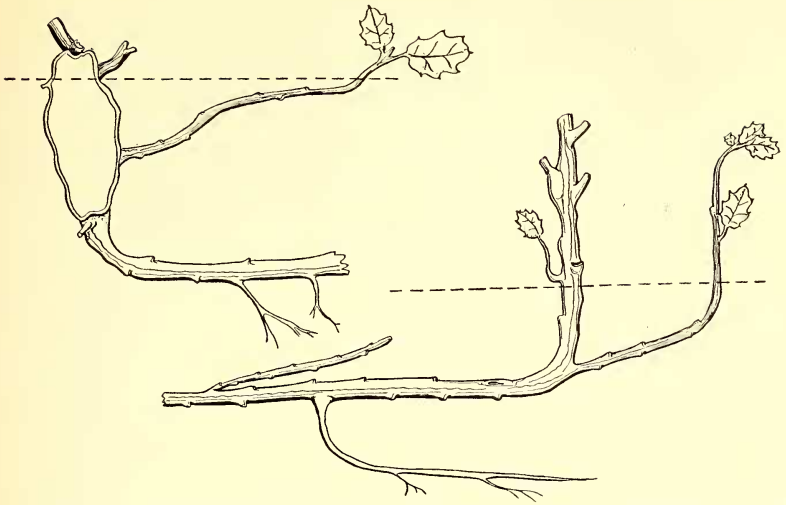

FIG. 1. *Quercus Hinckleyi:* single adult stems with attached rhizomes extracted from clumps.

THICKETS OF QUERCUS HAVARDI

Quercus Havardi Rydb. is the dominant of extensive shinneries[3] occupying the sand hills and rolling plains of the southern Great Plains region. It ranges, wherever a deep sand substratum exists, from southeastern New Mexico across the Panhandle of Texas to southwestern Oklahoma. In addition to extensive reconnaissance, detailed observations on this species were made in Ward and Wheeler counties, Texas.

The habit of *Quercus Havardi* is strikingly rhizomatous. A multitude of simple or sparsely branched shoots issues from the ground and grows to a height of 3 to 8 dm. Occasional much taller individuals are of hybrid origin (Muller, 1951). Upon examination of an unbroken thicket of these shoots, it is readily determined that each arises as an elongated rhizome which assumes a vertical direction of growth upon reaching the soil surface. The rhizomes range in length from 1 to 8 or 10 dm. The vigor with which a single individual spreads its rhizomes and multiplies its aerial shoots is reflected in the large size of the resulting clones. Close attention to minor differences in color, leaf size and shape, etc. clearly reveals the limits of individual clones. These sometimes form a mosaic of patches from 3 to 15 m. or more

[3] *Shinnery* is an adulteration of the French word *chênière*, still employed in Louisiana to indicate a place occupied by oaks (Penfound and Hathaway, 1938). Neither term is confined to the low shrubs referred to erroneously and redundantly as "shin-oaks" through the mistaken notion that the human tibia is somehow involved. The error is given credence through the coincidental shin-high stature of some oaks, and the adulterated term has thus been restricted in some localities to dwarf species.

in diameter, each clone in direct contact with its adjacent neighbors.

The failure of one clone to penetrate another (unless death of the plant leaves the soil unoccupied) indicates the tenacity with which the sites are held by the clones. Stems greater than 2 cm. in diameter are rare, and the greatest age revealed by terminal bud scar counts was eleven years. Individual dead shoots amongst the hundreds forming a clone are occasionally observed, but the resulting opening is so promptly closed by the growth of new shoots that ragged thickets seldom appear.

The clones of *Quercus Havardi* are not so luxuriant and dense where they are subject to heavy competition by grasses. The rhizomatous habit, however, spreads clones widely under these conditions also. Fracture of rhizomes under these circumstances frequently results in the division of a single clone to form several distinct individuals, sometimes eventually at some distance from one another.

In the course of a wide and detailed study of the species, *Quercus Havardi* was never observed to assume any habit other than a freely branching rhizomatous one. Age has no significance to an individual of this species except that it offers greater opportunity to spread and multiply by fracture. Senescence is limited to individual aerial shoots, and the entire clone is characterized by continuous rejuvenation. Seed production is usually copious, but the establishment of seedlings is rare except in disturbed areas where the young plants are relieved of competition of both the grasses and the parent shrubs. The two important consequences of the rhizomatous habit, then, are the much increased longevity of the individual and the multiplication of individuals under conditions of competition too severe for seedling establishment.

Mottes of Quercus virginiana

Quercus virginiana Mill. occurs on the coastal plain of Texas as a tree reaching great age and enormous size. Trunks 1 to 2 m. in diameter are not uncommon. It was early noted by settlers in this region that this species grew in even-aged clumps upon the rolling hills and coastal plain. Such an isolated clump of trees was termed a *motte*.[4] The term is used rather indiscriminately to designate a clump of half a dozen individuals or a grove covering a half dozen acres, only the qualifying adjectives "little" and "big" being employed to distinguish such extremes. The smaller mottes are by far the most common, however, and the term has therefore gained specificity to some degree.

[4] *Motte* is a French word meaning lump, clod, or hillock. The similarity of an isolated small grove of trees on a plain to such a concept led to its application. It is still being used in this sense quite correctly throughout south Texas although its origin is almost entirely forgotten.

In addition to the normally uniform trees comprising a motte, one usually observes nearby one or several patches of juvenile *Quercus virginiana* of various sizes and ages. An examination of several such patches 3 miles west of Cuero, DeWitt County, Texas, was undertaken. The soil was a rather heavy fine sandy clay loam of the Goliad series and bore a grass cover badly depleted by over-grazing. Similar patches in lightly grazed short-grass and prairie associations have been observed over a wide area in this region.

Excavation of the juvenile shoots revealed that all the shoots of a single patch were connected by an intricate system of interlacing rhizomes about 5 to 10 cm. beneath the surface (fig. 2A). In some instances the rhizomes were as much as a meter in length between organically connected adjacent aerial shoots. However, these rhizomes were criss-crossed by others which similarly bore aerial shoots so that proximity of shoots was no indication of closeness of organic connection. Yet, all the rhizomes eventually connected with one another within a single patch so that this represented a single individual (fig. 2B).

One such patch contained (1) a dead stump about 2 cm. in diameter to which two rhizomes were still attached, (2) one aerial shoot 0.5 m. in height, (3) an assortment of twenty-odd shoots ranging from a few centimeters to 2 dm. in height. Another much smaller patch contained one aerial shoot 2 dm. tall and several only a few centimeters tall. Older and larger patches formed thickets too heavy for ready excavation, but amongst shrubs 2 to 3 m. tall rhizomatously attached shoots were observed.

The patches of juvenile shoots ranged in diameter from 1 to 4 or 5 m., the larger size being correlated rather closely with the taller and older shrubs. Adjacent mottes of young trees (7 to 10 m. tall with trunks 1 to 2 dm. in diameter) had basal diameters of 2 to 6 m. Thus, an almost complete series was observed relating the juvenile patches of organically connected shoots to the adult mottes of apparently distinct trees. The isolated mottes, then, are clones derived from the rhizomatous action of seedlings (fig. 2C). The length of time such a clone remains in the shrub stage will depend upon the frequency with which aerial shoots are destroyed, mechanically or by grass fires. The resistance of the rhizomes to injury thus insures the survival of the clone through the critical period which terminates with the assumption of the tree-habit. Larger mottes are possibly formed by the confluence of adjacent small ones.

Rhizomatous Habit of Quercus pyrenaica and Quercus Ilex in Spain

The two common oaks north of Madrid, Spain, are *Quercus pyrenaica* Willd. and *Q. Ilex* L. In August, 1950, a visit to this area permitted a cursory examination of both species. There was no opportunity to make excavations, but several road cuts

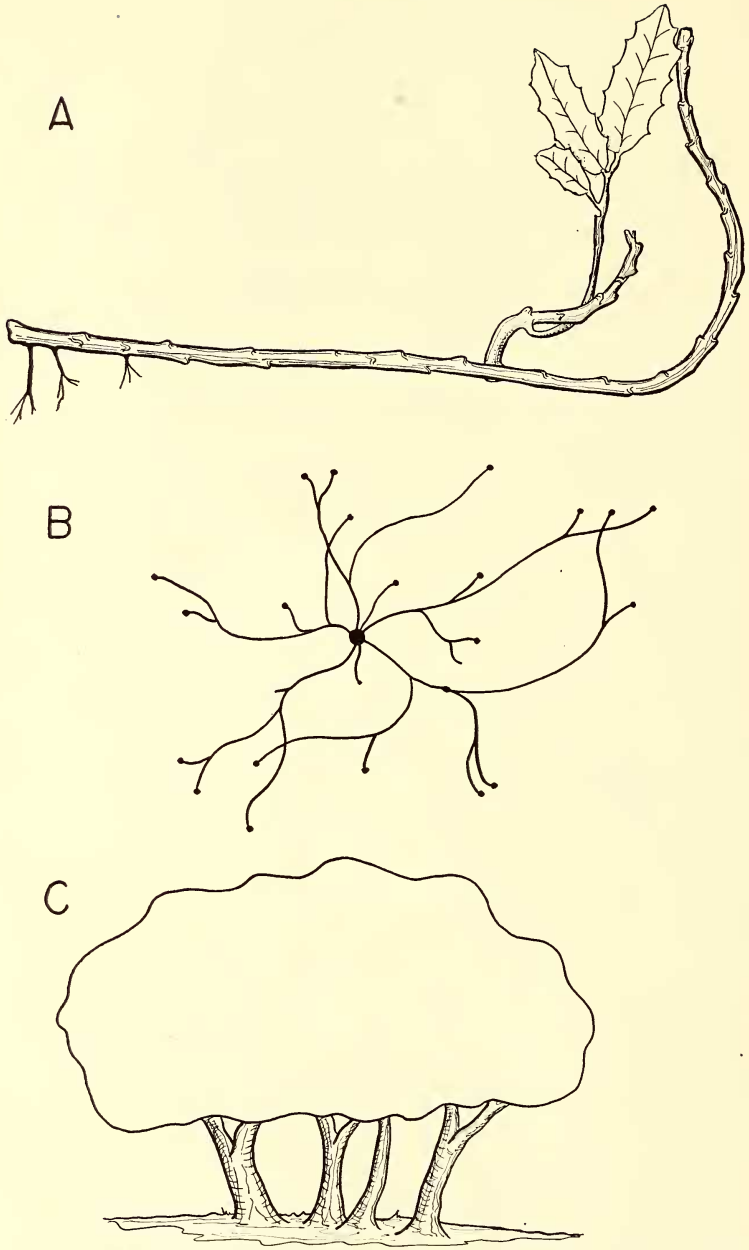

Fig. 2. *Quercus virginiana: A,* a portion of a juvenile rhizome exhibiting branching; *B,* a diagrammatic representation of the distribution of rhizomes in a single clone (the black dots indicating loci of aerial shoots); *C,* a small motte of young trees.

through masses of shoots were examined. These species occur abundantly on both rocky slopes and areas of flat soil. The small trees long have yielded fuel to the wood gatherers. The Spanish custom of trimming off the lower branches has spared many of these trees until senescence and repeated injury finally killed the trunks. Meanwhile, however, the partially or wholly decapitated trees have produced large numbers of shoots from the base of the trunk as well as at some distance from the trunk. Although *Quercus Ilex* was observed to produce more numerous shoots covering a greater area about the stump or trunk than *Q. pyrenaica,* and *Q. pyrenaica* sometimes produced clumps of trunks rather than single trunks, the two species are so similar in respect to the sprouting habit that they may be discussed jointly.

Where the trees occurred on eroded slopes it is likely that at least some of the sprouts arose as *retoños* induced by injury to exposed roots. However, the numerous individuals observed on level and undisturbed soil could not have experienced such root injury. Similarly, although felled and partially decapitated trees would be expected to produce stump sprouts as described by Jepson (1910) for so many of their California relatives, the many undisturbed mature trees observed in Spain exhibiting a wide circle of shoots at some distance from their bases are not of this class. The road cuts examined showed clearly the rhizomatous connections between individual shoots of various sizes and established the origins of these. This instance, then, is entirely comparable to the rhizomatous spreading commonly observed in *Quercus Brewerí* of California and numerous other species. It differs principally in the fact that the rhizomatous shoots of *Q. pyrenaica* and *Q. Ilex* are produced after tree habit is assumed.

Discussion

It is clear from the cases described that the various species of *Quercus* differ widely in the form of rhizomatous sprouting exhibited. Four general classes (exclusive of stump sprouting) have been described as follows: (1) short rhizomes in *Q. Hinckleyi,* (2) long rhizomes in *Q. Havardi,* (3) juvenile rhizomes of long duration terminated by tree-habit in *Q. virginiana,* and (4) rhizomes from mature trees in *Q. pyrenaica* and *Q. Ilex.* Although usually only one example was described in each of the four classes, it is noteworthy that one form or another of the rhizomatous habit is demonstrable in a wide variety of shrubby American species. A few of these are *Q. Brewerí* Engelm., *Q. dumosa* Nutt., *Q. Gambelii* Nutt., *Q. Mohriana* Rydb., *Q. oleoides* var. *quaterna* Muller, *Q. pungens* Liebm., *Q. pungens* var. *Vaseyana* (Buckl.) Muller, *Q. turbinella* Greene, *Q. undulata* Torr., and *Q. vaccinifolia* Kellogg, all in the Southwestern United States (from Texas to California). Scores of Mexican and several Atlantic region species might be added to the list.

The ecological significance of clonal spread is great in any semi-arid region unfavorable to seedling establishment. Not only is reproduction and invasion thus accomplished without the aid of the hazardous seeding process, but rejuvenation of short-lived individuals may thus be prolonged indefinitely. This increase in longevity is particularly important where competition with more xerophytic forms is intense. In this connection, it is noteworthy that in semi-desert regions the common woody associates of rhizomatous *Quercus* species with rare exceptions also exhibit the bush habit and rejuvenation by sprouting.

The exceptionally wide geographic occurence of the rhizomatous habit coincides significantly with the semiarid climates of the regions involved. Although wide variations in climate exist amongst central Spain, western Texas, and southern California, they are all characterized by long periods of deficient soil moisture in summer. However, there exist outstanding exceptions to this coincidence of the rhizomatous habit of oaks with semi-arid climate. Notable amongst these are *Quercus minima* on the sandy coastal plain in Florida, *Q. Margaretta* Ashe on sand beds of the Gulf coastal plain, and *Q. ilicifolia* Wang. confined to sandy barrens and rocky hills in the northeastern United States. It must be emphasized, however, that the number of species constituting such exceptions is small and that the plants involved are confined largely to edaphically adverse habitats.

In problems of taxonomic use of habital differences, the life history of the plant may be of distinct importance. Small's distinction of *Quercus minima* from *Q. virginiana* quoted above may or may not have been justified, but his employment of habit was unfortunate. The elements of the life history of *Q. virginiana* here described would cast doubt upon the taxonomic significance of habit in the southern live oaks.

An equally important significance of the rhizomatous habit is the role of the resulting longevity in determining evolutionary rate. Genetic processes of definite rate operate in a breeding population to a degree proportional to the frequency of sexual reproduction. Apomictic behavior in vegetatively reproducing clones is no different in this respect from apomictic seed production and results in a similar marked depression of sexual frequency. Thus, long-lived clones can serve to preserve a population in which a genetic difference has arisen or they can so restrict the rate of introgression as to postpone indefinitely the swamping of one species by another.

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A NEW FRITILLARIA FROM OREGON

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In southwestern Oregon and northwestern California—that area known by all West Coast taxonomists as rich in endemics—one of the most conspicuous wayside flowers is that of the "red bell", "red lily", or "scarlet fritillary", *Fritillaria recurva* Benth. No species of this genus thus far described from Western America approaches it in brilliance of color.

In 1941, however, Mr. L. G. Gentner, entomologist and assistant superintendent of the Southern Oregon Branch Experiment Station at Medford who, with his wife and two daughters perhaps comes nearer knowing every inch of Jackson and Josephine counties with their insects and plants than any other person in the state, reported what appeared to him an undescribed species of *Fritillaria.* The previous year his daughter Laura had brought in for her garden a plant supposed to be the common "red bell", but which, when it flowered, was noticeably different from *F. recurva.* The area, however, from which it had been collected was by this time forgotten. Numerous trips were made by the family in an endeavor to find the plant, but not until Katherine, another daughter, recognized the new lily in a flower arrangement at the home of a friend, was the original location rediscovered in the vicinity of Jacksonville.

As brilliant in color as *F. recurva,* the blossom of this new form is consistently of a different shade of red; its flowering period begins two weeks later; the plant is typically more robust; and the flower shape so different that regardless of other dissimilarities, plants of the two entities can readily be distinguished from a car moving rapidly on the highway.

Since the first report, it has been possible to make intensive studies of plants of both forms in all stages, not only in the field and from generous collections provided by Mr. Gentner, but also from plants grown at the Oregon State College Herbarium and in the Gentner garden. As a result of these studies, the "new" form appears, in the morphology of the flower as well as in the superficial aspects of the plant previously mentioned, so distinctly